Microtus richardsoni. By Daniel R. Ludwig

Microtus richardsoni (DeKay, 1842)

Water Vole

Arvicola richardsoni DeKay, 1842:91. Type locality "near the foot of the Rocky Mountains." Bailey (1900:60) stated that the type was obtained by Drummond near Jasper House, Alberta, Canada.

Arvicola (Mynomes) macropus Merriam and Stejneger, 1891:60. Type locality Pahsimeroi Mountains, 9,700 ft, Custer County, Idaho.

Aulacomys arvicoloides Rhoads, 1894b:182. Type locality Lake Keechelus, 8,000 ft, Kittitas Co., Washington.

Microtus principalis Rhoads, 1895:940. Type locality Mt. Baker Range, 6,000 ft, Westminster District, British Columbia.

CONTEXT AND CONTENT. Order Rodentia, Suborder Myomorpha, Family Muridae, Subfamily Microtinae (Arvicolinae according to some authors), Genus *Microtus*, Subgenus *Aulacomys*. *M. richardsoni* is included in the subgenus *Aulacomys* (Honacki et al., 1982; Rhoads, 1894a; Walker et al., 1975).

Recognized subspecies are (Hall, 1981):

M. r. arvicoloides (Rhoads, 1894b:182), see above (*principalis* Rhoads a synonym).

M. r. macropus (Merriam and Stejneger, 1891:60), see above.

M. r. myllodontus Rasmussen and Chamberlain, 1959:54. Type locality head of Boulger Canyon, 2 mi NE Huntington Reservoir, 10,000 ft, Wasatch Plateau, Sanpete Co., Utah.

M. r. richardsoni (DeKay, 1842:91), see above.

DIAGNOSIS. Except for the muskrat, *Ondatra zibethicus*, the water vole is the largest arvicoline rodent within its geographic range (Fig. 1). In the field, young and overwintered adults can be distinguished from other voles by their large hindfeet (≥ 23 mm). There are five plantar tubercules on the hindfeet (Miller, 1896) and both sexes have prominent flank glands (Quay, 1968).

The skull is large, massive and angular (Fig. 2). The wide zygomatic arches are strongly developed. The auditory bullae are reduced and not filled with spongy bones. The rostrum is slender; the incisive foramina are relatively small and constricted laterally. The paraoccipital processes are well developed, and the mandible also is constructed ruggedly (Banfield, 1974; Maser and Storm, 1970).

The dentition is robust and the incisors protrude noticeably. The first lower molar (m1) normally contains a posterior transverse loop followed anteriorly by five closed triangles and a terminal transverse loop that is constricted in the middle (Fig. 2). The last upper molar (M3) has an anterior transverse loop, a closed triangle on each side, and a short terminal loop (Bailey, 1900; Miller, 1896; Rhoads, 1894b).

GENERAL CHARACTERISTICS. Standard external measurements (mm) are: total length, 198 to 274; length of tail, 66 to 98; hindfoot, 25 to 34; length of ear from notch, 15 to 20 (Banfield, 1974; Hall, 1981). Mean body lengths (head and body) and weights of overwintered males are larger than those of overwintered females. Mean (± *SE*, range, *n*) body lengths (mm) and body weights (g), respectively, for overwintered adult males were 159.0 ± 7.1, 125 to 178, 86, and 113.7 ± 1.7, 72.0 to 150.0, 86; and for overwintered adult females were 150.9 ± 8.6, 125 to 165, 142, and 98.9 ± 1.3, 68.0 to 140.0, 145.

The pelage is long with the upperparts grayish sepia to dark sepia or dark reddish brown, often darkened with black-tipped hairs. The fur on the underparts is plumbeous, with white or silvery-white wash. The bicolored tail is dusky above and grayish below (Hall and Cockrum, 1953).

Cranial measurements (mm) are: basilar length, 29.0 to 34.8; zygomatic breadth, 19.0 to 21.8; least interorbital breadth, 4.5 to 5.0; mastoid breadth, 14.7 to 15.9; nasal length, 9.0 to 9.8; alveolar length of upper molars, 8.0 to 8.5; basiocranial depth over bullae, 10.8 to 11.2; length of palatal bridge, 7.0 to 7.8; length of incisive foramina, 5.3 to 6.1; and postpalatal breadth, 11.3 to 12.5 (Anderson and Rand, 1943; Durrant, 1952; Rasmussen and Chamberlain, 1959; Rhoads, 1894b).

The teeth are prismatic and unrooted. The dental formula is i 1/1, c 0/0, p 0/0, m 3/3, total 16.

Quay (1954) suggested that the degree of development of the inflexal flaps of the upper lip, the posteriorly situated naso-palatine canal openings, and the posterior shift of the anterior limit of the incisive foramina perhaps were correlated with the aquatic habits of the water vole.

DISTRIBUTION. The geographic range of the species forms two disjunct bands through six states and two provinces in northwestern North America (Fig. 3). The westernmost portion of the range extends southward through the Coast Mountains of western British Columbia and both the Blue and Cascade mountains of Washington and Oregon. The eastern and larger portion of the range extends southward from the Rocky Mountains in southeastern British Columbia and southwestern Alberta, through western Mon-

FIGURE 1. Photograph of an overwintered adult male *Microtus richardsoni richardsoni* from Alberta, Canada. Note the large flank gland.

FIGURE 2. Dorsal, ventral, and lateral views of the cranium, and lateral and occlusal views of the mandible of an overwintered adult male *Microtus richardsoni richardsoni* from Plateau Mt., 99 km SSW of Calgary, Alberta, Canada. Greatest length of skull is 30 mm.
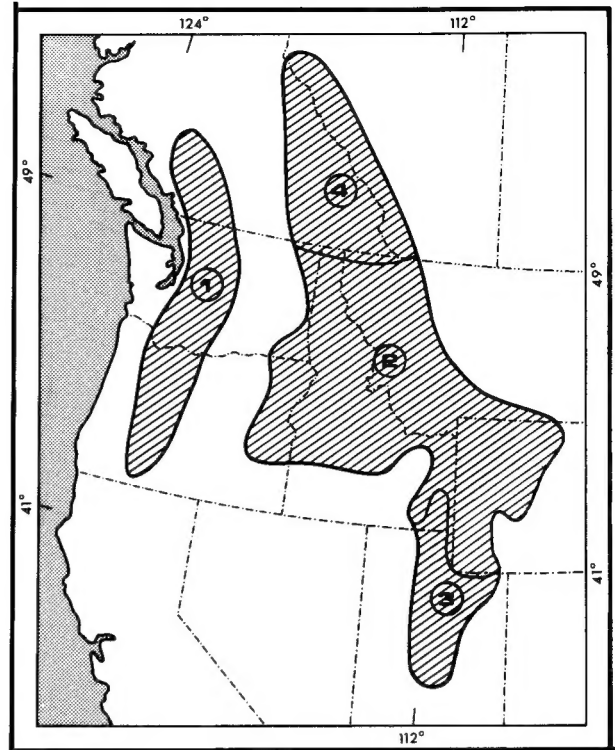

FIGURE 3. Geographic distribution of *Microtus richardsoni* in North America: 1, *M. r. arvicoloides*; 2, *M. r. macropus*; 3, *M. r. myllodontus*; 4, *M. r. richardsoni*. Figure redrawn from Hall (1981).

tana, western Wyoming and the upper two-thirds of Idaho and into central Utah.

Water voles generally occur at elevations from 1,524 to 2,378 m in Canada (Banfield, 1974) and 914 to 3,201 m in the United States (Hall, 1981). Racey (1960) and Taylor and Shaw (1927) reported unusually low elevation records of 183 m (British Columbia) and 549 m (Washington), respectively. Locally, the geographic distribution of the water vole is highly discontinuous. Large expanses of coniferous forest, mountain slopes, and valleys present seemingly insurmountable barriers to overland movement between occupied habitats.

The present habitat requirements of *M. richardsoni* suggest it was an occupant of the tundra region bordering the Cordilleran glacial front. The geographic range presumably was limited during the post-Pleistocene period as the species spread northward into the Rockies and followed the retreating tundra-like vegetation into high montane areas (Banfield, 1958; Dalquest, 1948; Findley and Anderson, 1956; Hoffmann and Taber, 1967).

FOSSIL RECORD. *Microtus richardsoni* is known from the Holocene and late Pleistocene. Specimens were recovered in Montana (Rasmussen, 1974), Wyoming (S. A. Chomko, in litt.) and Alberta (Burns, 1982). *M. richardsoni* is considered a primitive *Microtus* that originated from an ancestral form of *Mimomys* in Siberia (C. A. Repenning, in litt.).

FORM. Both sexes possess a pair of flank glands (Anderson and Rand, 1943; Bailey, 1900, 1936; Hollister, 1912; Miller, 1896). The glands are large and compact subdermal masses of lipid-secreting cells (Quay, 1968). Flank glands are clearly visible in captive-born young at 33 days of age (Skirrow, 1969). Glands are apparent on field-captured young as small as 90 mm (head and body) and 19 g.

Flank glands show a positive correlation with body mass in all age classes, and a seasonal pattern of enlargement during the breeding season. When the glands are hypertrophied, the hair covering them is greasy and matted. As the breeding season ends, the gland regresses, dries, and sloughs off, and new hair erupts from the gland surface (Ludwig, 1981).

There are eight mammae, two pairs pectoral and two pairs inguinal (Bailey, 1900; Miller, 1896).

The stalk of the baculum is broad and relatively flattened and has a single median ossified process (Anderson, 1960). The base of the main bone is large and usually triangular with a pronounced proximomedial point. Viewed ventrally its proximal outline decurves between that point and the lateral prominences. Generally there is a moderately sharp incurve as the base joins the shaft, that tapers gradually distally, then enlarges to a rounded head. The medial rod is a small cone closely appressed to the head of the proximal bone. The medial rod arches ventrally and lacks lateral digits. Mean measurements ($n = 3$) of baculum lengths were: proximal bone 4.5 mm, medial rod 1.1 mm and medial ossicle 0.9 mm (Hooper and Hart, 1962).

Hooper and Hart (1962) illustrated the glans penis and described it as follows: the dorsal lobe is indistinct and rimmed with papillae. The ventrolateral sectors are strongly papillose and the entire circumference of the rim may bear from 34 to 42 fingers, all roughly of equal height. The dorsal papilla consists of two spine-tipped conules. The lateral bacular mounds are small and scarcely discernible and engulfed in folds of tissue from the large medial mound. The urethral process is composed of two large pointed lobes, each with two spines on its medial edge and one on its distal tip. These lateral lobes are separated by a minute medial knob. The mean measurements of the glans penis ($n = 3$) were: diameter 3.4 mm and length 5.5 mm.

FUNCTION. Bradley (1976) examined the bioenergetics and thermoregulatory abilities of *M. richardsoni* and six other North American microtines under laboratory conditions. The values obtained for the water vole, the largest species tested, were: standard metabolic rate (SMR), $\bar{X} \pm 2\ SE = 1.74 \pm 0.08$ cc O_2 g^{-1} h^{-1}; whole animal metabolic rate (MR), $\bar{X} \pm 2\ SE = 89.03 \pm 5.33$ cc O_2/h; daily energy utilization, 16,433 cal; daily caloric equivalent, 12,942 cal/day; assimilation efficiency, 80.5 $\pm$ 0.7%; body temperature, $\bar{X} \pm 2\ SE = 38.7 \pm 0.23$°C ($n = 15$); total minimum thermal conductance, 0.117 ± 0.003 cc O_2 g^{-1} h^{-1} °C^{-1} and weight independent conductance, $\bar{X} \pm 2\ SE = 0.912 \pm 0.032$ cc O_2 $w^{-0.48}$ h^{-1} °C^{-1}.

The standard metabolic rate was 133% of the predicted metabolic rate for water voles. Water voles had a lower caloric intake per gram of body weight than expected and showed the greatest digestive efficiency of seven species. The thermal conductances of all species were lower than predicted values. *M. richardsoni* had the lowest thermal conductance, and showed the largest deviation from the predicted value and the lowest percent (92.4%) of the predicted value. The lower end of the thermal neutral zone or lower critical temperature for water voles was 24.0°C. Body temperature was independent of ambient temperature from at least as low as 2°C to 29°C. In *M. richardsoni*, evaporative cooling contributed more to heat dissipation (14.6%) than in any other species (Bradley, 1976).

Body mass and body length data from young ($n = 9$) captured during their first winter indicated that growth continued during winter. Young of both sexes showed a net increase in both length and mass, and were of adult size (head and body length 140 mm; ≥70 g) by the spring melt (Ludwig, 1981).

REPRODUCTION AND ONTOGENY. Water voles conform to the basic microtine pattern of induced estrus, postpartum estrus, and lactational pregnancies (Hasler, 1975). Induced estrus and postpartum estrus within 24 h of parturition were observed in a laboratory colony of water voles (Jannett et al., 1979). These workers had an insufficient number of females to demonstrate induced ovulation, but their observations did not support the occurrence of spontaneous ovulation. Brown (1977) found that ovulation by water voles in late May or early June appeared to coincide closely with the appearance of the first green herbaceous vegetation as melting snowbanks receded. A minimum gestation period of 22 days was observed for four females (five litters) in the laboratory (Jannett et al., 1979). Field-caught animals indicated the occurrence of postpartum ovulation and lactational pregnancies, with postpartum gestations prolonged (Brown, 1977). Successful postpartum estrus occurred in the laboratory (Jannett et al., 1979), but the timing and duration of postpartum estrus in the field is unknown.

The breeding season extended over 3 months from early June through August (Anderson et al., 1976; Ludwig, 1981; R. D. Taber, in litt.; Taylor and Shaw, 1927). However, breeding activity sometimes began in late May and continued into September (Ludwig,

1981). Births were reported from June until late September (Brown, 1977; Cowan and Guiget, 1956; Soper, 1973; R. D. Taber, in litt.). Both Ludwig (1981) and Pattie (1967) reported that the first capture of young usually occurred after 1 July each year.

Young of both sexes are reported to mature sexually and reproduce in the breeding season of their birth (Anderson et al., 1976; Crowe, 1943; Ludwig, 1981; Negus and Findley, 1959; Pattie, 1967; R. D. Taber, in litt.). However, overwintered adults are responsible for most reproduction. Only 25% of all young captured were reproductively active in their first year (Ludwig, 1981).

Overwintered adult males become reproductively active earlier and remain reproductively active longer than overwintered adult females. Although some overwintered adult females may produce a second litter, no more than two litters are produced by most overwintered females in one breeding season. Some young females that produced a litter in their first summer also may reproduce the following spring (Ludwig, 1981).

Most estimates of mean litter size are between five and six (range 2 to 10). The mean litter sizes ($\pm SE$) reported based on embryo (E), placental scar (P), and corpora lutea (C) counts are: Alberta, (P) 5.42 ± 0.58, $n = 12$, (E) 5.17 ± 0.44, $n = 19$ (Ludwig, 1981); British Columbia, (E) 7.00, $n = 3$ (Racey and Cowan, 1935), (E) 7.33, $n = 3$ (Anderson and Rand, 1943); Montana, (E) 5.59 ± 0.28, $n = 37$, (P) 6.35 ± 0.32, $n = 23$, (C) 5.91 ± 0.24, $n = 46$ (R. D. Taber, in litt.), (E) 5.60, $n = 16$, (P) 7.10 ± 0.34, $n = 7$ (Pattie, 1967), (E) 7.85 ± 0.51, $n = 26$ (Brown, 1977); and Wyoming, (E) 6.00, $n = 10$ (Negus and Findley, 1959), (E) 5.60, $n = 20$ (F. J. Jannett, in litt.).

The placental scar counts always are slightly larger (<1.0) than embryo counts, suggesting either the production of more than one litter per overwintered female per season, or the occurrence of some prenatal mortality. The duration of placental scars in *M. richardsoni* is unknown.

Mean litter size increases with age and reproductive experience (Ludwig, 1981; R. D. Taber, in litt.). Litter size does not show a significant correlation with either altitude or latitude (Ludwig, 1981).

Captive young grow at a rate of 26.1% of the birth mass/day, or gained an average of 1.24 g/day. Growth was linear for the first 33 days. The animals were still not sexually mature at the end of this period (Skirrow, 1969).

Young were born naked and blind, and weighed about 5 g. Newborn young could vocalize. By day 3 after birth, sparse fur covered the body and the pinnae were free from the head. White fur began to appear on the belly by day 4 postpartum. The incisors erupted by day 6. Pups ran and climbed by 10 days of age. The eyes opened at 12 days and young could run swiftly. Captive young swam voluntarily on day 17 and were weaned by day 21. The testes were descended by 38 days. Captive young still nested together at 32 days, but nested singly by 40 days. Young males appeared to court by 60 days (Skirrow, 1969).

ECOLOGY. The water vole characteristically is found in the Canadian and Hudsonian life zones within subalpine and alpine meadows in close proximity to water, especially swift, clear, spring-fed or glacial streams with gravel bottoms. *M. richardsoni* was found along the edges of high-elevation ponds (Bailey, 1918; Soper, 1964) and marshes (Dalquest, 1948).

Most ecological information of *M. richardsoni* is a by-product of museum collecting trips and field observations (Findley, 1951; Hall, 1931; Hoffmann et al., 1969; Hooven, 1973; Lechleitner, 1955; Long, 1965; Maser and Hooven, 1970; Rand, 1948; Richardson, 1829). Population characteristics and life history traits were examined during only three field studies of the species (Anderson et al., 1976; Ludwig, 1981; Pattie, 1967).

The water vole is unusual among microtine rodents because of its large body size, limited geographic range, high degree of habitat specificity for small habitat patches bordering high elevation mountain streams, and small population numbers. Breeding season densities (voles/ha) of 8.1 to 32.5 (Anderson et al., 1976), 0.2 to 12.2 (Ludwig, 1981), 0.1 to 1.0 (Pattie, 1967) and 4.5 to 24.7 (R. D. Taber, in litt.) were reported from streamside habitats.

Seasonally, populations were reported to increase from 1.8 to 7.2 (Ludwig, 1981) and <1.0 to 4.0 times (R. D. Taber, in litt.). Although quantitative data were not provided, "population explosions" were reported during 1927, 1949, and 1958 in British Columbia (Racey, 1960) and during 1973 in Washington (M. L. Johnson, pers. comm.).

Only overwintered adults usually are present at the time of the June snow melt in Alberta (Ludwig, 1981). Young-of-the-year first entered the trappable population in the second or third week of July, and a second group of young appeared above ground in August.

Gross mortality (that is, mortality and emigration of young between their first and second summer) ranged between 71.4 and 100%. The age distribution of several populations indicated a 1:1 or greater replacement of adults by young. The proportion of adults in populations ($n = 3$; data pooled over 3 years) dropped to 53.4% in July, 40.9% in August and 24.1% in September (Ludwig, 1981).

Most individuals overwintered only once and died in their second fall or winter. Of 27 adults captured at one study site over a 3-year period, 88.9% disappeared by the end of September each year. The life span of one female captured shortly after birth and radio-tracked as an adult was estimated at 16 months (Ludwig, 1981). Some animals survived two winters (Ludwig, 1981; Pattie, 1967).

Other species of small mammals captured within areas occupied by water voles include *Sorex palustris, S. cinereus, S. bendirii, S. monticolus, S. hoyi, Microtus longicaudus, M. montanus, M. pennsylvanicus, Clethrionomys gapperi, Synaptomys borealis, Phenacomys intermedius, Zapus princeps, Thomomys talpoides, Tamias amoenus,* and *Spermophilus columbianus* (Anderson, 1959; Anderson et al., 1976; Hooven, 1973; M. L. Johnson, pers. comm.; Ludwig, 1981; Negus and Findley, 1959; Pattie, 1967; Salt, 1978). Many of these species used water vole runways.

The water vole is not known to be a major prey species in the diet of any carnivore. It is known to be taken by short-tailed weasels (*Mustela erminea*), martens (*Martes americana*), and perhaps accipters (Accipitrinae; Ludwig, 1981; D. Pattie, pers. comm.; Salt, 1978).

Ectoparasites include fleas, *Catallogia chamberlini, Haemoymasus alaskensis, H. liponyssoides, Nearactopsylla hyrtaci, Monopsyllus eumolpi eumolpi, Megabothris abantis, M. asio megacoplus, Peromyscopsylla selenis, P. homifer homifer;* and mites, *Haemogamsus nidiformes, Hirstionyssus isabellinus, Laelaps alaskensis* and *Euryparasitus* sp., near *emarginatus* (Holland, 1949; Kinsella and Pattie, 1967; Ludwig, 1981). A cestode belonging to the genus Andrya was reported from one wild-caught animal (Ludwig, 1981).

Overwintered adult males (64.0% of 50 animals) had more wounds than other sex and age classes suggesting that they were involved in more aggressive and perhaps a greater number of intraspecific interactions. Seventy-six percent of all adult males ($n = 42$) had at least one wound as opposed to only 6.0 to 20.0% of the other sex and age classes. Overwintered adult females with wounds were found only when population numbers were high. The mean number ($\pm SE$) of wounds per vole (Ludwig, 1981) was: adult males, 2.33 ± 0.34 ($n = 32$); adult females, 1.43 ± 1.33 ($n = 10$); young males, 2.33 ± 1.33 ($n = 3$); and young females, 1.60 ± 0.40 ($n = 5$).

Leaves and occasionally stems of forbs are the major foods of water voles. Grasses, sedges, and willows also are eaten. Species composing the diet differ throughout the range of *M. richardsoni* (Anderson et al., 1976; Cowan and Munro, 1945; Hollister, 1912; Ludwig, 1981; D. Pattie, in litt.; Racey and Cowan, 1935; Salt, 1978; Taylor and Shaw, 1927).

Taylor and Shaw (1927) noted the presence of *Vaccinium*, bulbs of *Erythronium*, and conifer seeds in the diet. Seed also was reported in the summer diet by Bailey (1936) and Salt (1978). Salt (1978) also found small amounts of insect matter and willow buds were eaten. Water voles likely feed on subterranean parts of plants throughout the year, but surface digging for roots and rhizomes was not observed by Ludwig (1981). Ludwig (1981) suggested that winter foods in Alberta consisted of dry aerial portions of herbaceous vegetation, plus preformed buds of perennials and roots, rhizomes, and corms. Winter foods are reported to include the roots of *Pedicularis*, willows (chiefly *Salix barrattiana*), *Erythronium gradiflorum, Arnica,* and *Antennaria* (Salt, 1978), and bear grass, *Xerophyllum tenax* (Taylor and Shaw, 1927). Ludwig (1981) found no evidence of food storage for winter.

BEHAVIOR. The water vole is not nearly as aquatic as the muskrat (*Ondatra zibethicus*), but swims and dives well and is best considered semi-aquatic (Audubon and Bachman, 1854; Bailey, 1936). Water voles maintain a diel activity cycle with peak activity during periods of darkness (Anderson et al., 1976; Ludwig, 1981; Racey and Cowan, 1935).

In areas where water voles occur, surface runways 5 to 7 cm wide pass through areas of herbaceous vegetation, willow, and moss. Runways parallel and criss-cross springs and streams that are incorporated into the runway system. "Resting platforms" and submerged and water-level burrow entrances are found along stream banks (Bailey, 1918, 1936; Cowan and Guiget, 1956; Cowan and Munro, 1945; Dalquest, 1948; Ludwig, 1981).

The well-worn appearance of exposed soil of surface runways and presence of droppings, cut segments of vegetation, and mounds of recently excavated soil indicate the presence of water voles. Small groups of droppings (1 to 20) are found occasionally along runway systems, on top of piles of freshly excavated soil, or at entrances to subterranean passages (Anderson et al., 1976; Ludwig, 1981).

Subterranean passages and nest chambers are excavated and re-excavated between June and late September. Tunnels are located immediately below the 4- to 6-cm thick network of plant roots and mosses that cover the soil surface. Short lengths of subterranean runways (≤ 1 to 3 m) and surface runways form branching systems that lead to nest chambers, feeding areas, and stream edges. Dimensions ($\bar{X} \pm SD$) of burrows and nest chambers (in cm) were: burrow diameter, 8.0 ± 2.0 ($n = 7$); chamber height, 9.5 ± 0.7 ($n = 2$); chamber length, 15.0 ± 6.4 ($n = 4$); and chamber width, 10.7 ± 0.9 ($n = 4$). Numerous openings in stream banks and close to streams allow easy access to areas above and below the soil surface. Radio-tracking suggested that interconnecting and blind tunnels served as temporary shelters, retreats, and feeding shelters (Ludwig, 1981).

Summer nests are located inside small rises in the microtopography, and beneath logs and stumps (Cowan and Munro, 1945; Ludwig, 1981). A large dome nest (inner cavity diameter of 7 cm) completely fills each nest chamber and is occupied by a single individual. Nests ($n = 5$) are constructed of short segments (2 to 5 cm) of leaves and stems of grasses (*Agropyron, Calamagrostis*), sedges (*Carex*), and rushes (*Juncus*) (Ludwig, 1981).

Microtus richardsoni lives beneath snow for 7 to 8 months each year. Subnivean tunnels are excavated through the snow (Dalquest, 1948; Taylor and Shaw, 1927). Tunnels run along the surface soil, but do not lead to the snow surface. Water vole activity was not observed above the snow surface after ≥ 6 cm of snow covered the ground (Ludwig, 1981). Taylor and Shaw (1927) suggested that water voles moved to winter habitats away from streamside areas. However, during three spring melts in Alberta, Ludwig (1981) found no evidence of above-ground activity in areas adjacent to streamside habitats.

Water voles occupy subterranean nests the year-round. Occasionally nests are found on top of the soil surface after the snow melts (Cowan and Munro, 1945; Dalquest, 1948; Ingles, 1965; Ludwig, 1981; Taylor and Shaw, 1927). These surface nests may be used either throughout the winter or only during the snow melt when many subterranean spaces become flooded.

Habitat descriptions lack quantified habitat characteristics (Anderson et al., 1976; Soper, 1964; R. D. Taber, in litt.). The mean ($\pm SD$) habitat width measured on one side of four streams was 14.7 ± 8.0 m ($n = 146$). Vole activity usually was restricted to within 5 to 10 m of stream banks, but animals moved further inland in areas where springs drained boggy areas and join streams (Ludwig, 1981).

Ludwig (1981) found that during the snow-free period, ground-level temperatures in water-vole habitats fluctuated with air temperature. However, beneath a snow cover, water voles were subjected to temperatures between -1.0 and $1.0°C$. A mean depth of ≥ 14 cm of new snow effectively shielded underlying soil from colder supranivean air and wind. The annual range of mean ground-level temperatures where water voles lived was $9.3°C$ (-0.4 to $8.9°C$), whereas air temperatures 1 m above the soil ranged over $26.0°C$ (-16.4 to $9.6°C$).

Overwintered females maintained minimally overlapping or non-overlapping home areas. When population numbers were low, overwintered females were scattered widely along streams. During years when local population numbers were large, overwintered females clustered in streamside areas but home-area overlap was minimal or nonexistent.

Overwintered females remained within small and exclusive home areas, whereas overwintered males moved along longer portions of stream and overlapped the seasonal ranges of both overwintered

females and males. When water voles were widely spaced along a stream and female density was low, males were less likely to remain in one streamside area and moved extensively between female ranges. When population densities were high, a male usually was found repeatedly in one area near a group of females. A polygamous mating system was suggested (Ludwig, 1981).

Ludwig (1981) calculated maximum intercapture distances (in m) for voles captured two or more times within one trapping session (MID) and during one breeding season (SMID). Mean MIDs ($\pm SE$) were: young females, 27.3 ± 3.4 ($n = 43$); overwintered adult females, 52.9 ± 11.1 ($n = 79$); young males 75.4 ± 28.8 ($n = 45$); and overwintered adult males, 132.7 ± 31.6 ($n = 38$). Mean SMIDs were: overwintered adult females, 93.8 ± 25.6 ($n = 33$); young females, 102.2 ± 35.9 ($n = 28$); young males, 200.8 ± 79.6 ($n = 20$); and overwintered adult males, 332.0 ± 82.7 ($n = 20$). Intergroup differences existed among both MIDs and SMIDs for the four sex and age classes. MIDs of overwintered adult males differed significantly from all other groups when compared individually with the three other groups, but the other three classes did not differ among themselves. For overwintered adult males, SMIDs were significantly larger than for either group of females.

Mean home range area ($\pm SE$) based on 72-h radio-tracking sessions were 222 ± 76 m² (19 to 1,018, $n = 16$) for overwintered adult females, and 770 ± 359 m² (129 to 3,419, $n = 9$) for overwintered adult males (Ludwig, 1981).

Young remain close to their natal site for varying lengths of time. Some individuals disappear from the trappable population within 1 month after emergence from the nest, but others establish themselves and breed within or near their birth site (Ludwig, 1981).

The manner by which home areas are maintained is not clear, but active defense via individual encounters and the deposition of olfactory cues is probable. Feces, urine, and secretions from flank glands deposited along runways and subterranean passages may be involved (Anderson et al., 1976; Jannett and Jannett, 1974, 1981; Skirrow, 1969). Jannett and Jannett (1974, 1981) described the use of flank glands to scent-mark (drum-marking and flank-rubbing) by adults during staged dyadic encounters.

GENETICS. *Microtus richardsoni* has a diploid number of 56 chromosomes and a fundamental number of 56 to 58. All autosomes are acrocentric and the X-chromosome is metacentric. Matthey (1957, 1969) considered the fundamental number to be primitive for microtines.

Anderson et al. (1976) found two populations were polymorphic at loci controlling leucine aminopeptidase (LAP), plasma esterases, and red-cell esterases. Variability was not detected in transferrins (Tf), hemoglobins (Hgb), or glucosephosphate isomerases. The level of intrapopulation variability (Tf, $n = 49$; Hgb and glusephosphate, $n = 38$) appeared relatively high, compared with that in other rodent species, despite subdivisions of populations into small groups isolated in small areas of favorable habitat.

When compared electrophoretically with four other North American species, and two Holarctic and two Siberian species, *M. richardsoni* seemingly was close to *M. pennsylvanicus*, but diverged from all other species of *Microtus* at the LAP locus. Six-phosphogluconate dehydrogenase (6PGD-A) was the predominant allele in *M. richardsoni*. The water vole displayed Tf in all specimens examined ($n = 17$), and possessed three leucine aminopeptidase alleles (LAP-E, LAP-F, LAP-G) not observed in other taxa. None of the LAP alleles prevalent in the other taxa examined was recognized. *M. richardsoni* generally showed low affinities with the Holarctic groups, but a high resemblance biochemically with *M. pennsylvanicus* sharing alleles at the Tf, G6PD, 6PGD, and Hgb B loci, and further resembled *M. pennsylvanicus* in lacking minor Hgb fractions (Nadler et al., 1978).

REMARKS. At the present time, generic relationships of the North American water vole require clarification; the species has been assigned to both *Arvicola* and *Microtus*. Many of the morphological resemblances (Anderson, 1960; Hooper and Hart, 1962; Jannett and Jannett, 1974; Miller, 1896, 1912; Quay, 1954, 1968; Zimmerman, 1955) may be interpreted as convergences between the Old World *Arvicola terrestris* and *M. richardsoni*. Corbet (1966) stated that *Arvicola* was restricted to the Palearctic, but Corbet (1978) noted the use of the generic name in association with *richardsoni*. Karyotypic (Chaline and Matthey, 1971; Chaline and Mein, 1979; Matthey, 1957) and paleontologic evidence (Chaline,

1977; Repenning, 1980) suggest that *M. richardsoni* is a primitive *Microtus* that originated from a *Mimomys* ancestral form in Siberia about 1.5 million years before *Arvicola* formed in Europe. Biochemical comparisons of *M. richardsoni* with Palearctic forms (Nadler et al., 1978) and a broadly comparative synthesis of all available types of data should clarify the generic affinity of the species.

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